

Further data on carpal structure in ranoid frogs

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An examination of the carpus in some species belonging to the Astylosterninae, Hyperoliinae, Raninae and Phrynobatrachinae confirms the previous hypothesis formulated by LAURENT (1951). The most plesiomorphic carpus observed in Ranoidea exists in some Astylosterninae and the Hyperoliinae. From this condition, a first phyletic line in which the 2nd distal carpal is fused with the Y element (or preaxial centrale), is represented by the Arthroleptinae. The other, in which the 3rd distal carpal is fused with the 4th and 5th distal carpals, occurs in the Ranidae, but some Astylosterninae show the same transformation (*Astylosternus* and *Nyctibates*)

INTRODUCTION

The carpus of anurans is composed of bones, of which the number and topographical relations vary according to the group. TRUEB (1973) and later DUELLMAN & TRUEB (1986) showed that there is a tendency toward a reduction in the number of elements, by loss or fusion, a fact which is obvious in advanced anurans like ranoids.

SHUBIN & ALBERCH (1986, in press) came out with a seemingly opposite ontogenetic model: a continuous initial structure and a subsequent segmentation, branching and secondary condensation. There is, according to their observations, a primary axis extending from the distal end of the ulna. It divides and branches itself into ulnare, distal carpals, 5, 4, 3, 2, and digit IV to II. However, the digit V results from a secondary condensation. There is also a radial axis, starting from the distal end of the radius and segmented into a radiale, the Y element and the prepollex. Thus, two strongly unequal embryonic structures are present from the beginning. The segmentations produce the configurations which appear in the primitive anurans, in which the number of carpal elements is highest. Then, some segmentation fails to occur (primary fusions) or some elements that never have been united merge, or that were initially fused, then segmented and finally fuse again (secondary fusions), determining the apomorphic carpi of the advanced frogs. According to this hypothesis, real paedomorphosis could be put forward to explain the most fused carpi, provided that those fusions were primary, contrary to what DREWES (1984) proposed about Hyperoliinae.

However, if two opposite processes are involved in the ontogeny of the carpus in frogs, i.e. one of segmentation, then one of fusions, any allochronic disturbance may, at first sight,

determine unexpected structures lending themselves to divergent interpretations. One can only hope that the primary phase of segmentation and the secondary phase of fusion remain widely separate in time so that no telescoping is likely. The fact that many authors (HOWES & RIDEWOOD, 1888; TRUEB, 1973; DREWES, 1984) have been able to propose a synthesis in which the polarity of the evolution of the carpus is from numerous towards less numerous elements is encouraging in this respect. Therefore, we chose to adopt their hypothesis, i.e. that by and large, the trend of evolution has been toward fusions of previously discrete elements.

The phylogenetic hypothesis that is the basis of this work is as follows: the Ranidae (Raninae, Phrynobatrachinae, Mantellinae, Rhacophorinae) is the sister group of the Arthroleptidae (Astylosterninae, Arthroleptinae, Hyperoliinae). Together they are the sister group of the Hemisotidae. All three are the sister group of the Microhylidae. Outgroups have not been considered here, because the junior author is preparing another study in which they will be.

Be that as it may, four distal carpals have been observed in *Pelobates* and *Megophrys*, whereas in *Pelodytes* the distal carpals 4 and 5 are fused (HOWES & RIDEWOOD, 1888). Such a condition has been observed by LAURENT (1941a, 1942) in Hyperoliinae and *Trichobatrachus* (Astylosterninae), observations confirmed by LIEM (1970). This did not prevent DREWES (1984) to state that the distal carpal 3 is fused with the distal carpals 4 and 5 in all Ranidae in which he included the Astylosterninae and the Arthroleptinae. He only saw the distal carpal 3 free in the Hyperoliinae, but he attributed the condition to paedomorphosis, which is unwarranted.

Subsequently, LAURENT & FABREZI (1985) re-examined the arthroleptine carpal structure, and discovered that in *Cardioglossa* (fig. 1b), both the distal carpal 2 and 3 are free; thus, the carpus is as primitive as that of Hyperoliinae and *Trichobatrachus*. The structures observed in *Arthroleptis* and *Schoutedenella* (fig. 1d) have been confirmed, i.e. fusion of the distal carpal 2 with Y element in *Arthroleptis* (fig. 1c), and the fusion of both distal carpals 2 and 3 with the Y element in *Schoutedenella* (fig. 1b). Thus, the six-element carpus of *Arthroleptis* might have been confused with the six-bone carpus of primitive ranids by DREWES, which would explain his error, but such an explanation does not apply to *Schoutedenella*, because the adults possess only five bones in the carpus. In view of the controversies involved, it seemed useful to us to investigate other Astylosterninae, Raninae and Phrynobatrachinae in order to see if the new data confirm the above mentioned scheme.

MATERIALS AND METHODS

Specimens examined are listed in Appendix. The specimens were cleared and double-stained with Alcian Blue and Alizarine Red S, following WASSERSUG's technique (1976). Observations were made with a binocular microscope. Both hands of each specimen were examined.

TERMINOLOGY

The terminology used by past authors is diverse. According to the structure of the chiropterygium (GREGORY, MINER & NOBLE, 1923), there are (1) a radial series (preaxial), the distal element of which is the prepollex, and (2) an ulnar series (postaxial) which includes all fingers and their respective carpals. With the exceptions of DUGES (1833) and HOWES & RIDWOOD (1888), all authors refer to the radial and ulnar as the proximal bones of the carpus. Some have called 1st centrale (LAURENT, 1940, 1941, 1942; LIEM, 1970; DREWES, 1984) and others (ANDERSEN, 1978; DAVIES & MARTIN, 1987) have called preaxial centrale the carpal distal to radial and similarly they called 2nd centrale and postaxial centrale, the carpal distal to ulnar. SHUBIN & ALBERCH (1986) claimed that the radial series includes the Y element (= preaxial centrale), and that the centralia of anurans are not homologous to the centralia of other vertebrates in which they originate by branching and segmentation from the intermedium, an element that is absent in the embryonic carpus of anurans. Therefore, according to SHUBIN & ALBERCH, anurans lack a postaxial centrale, and the external distal carpal includes only the 5th distal carpal.

Another controversial issue relates to the lost finger TRUEB (1973) reported the fifth digit to be absent. This interpretation has been also supported by JAROSOVA (1973) and DE SAINT-AUBAIN (1981). However, other authors (e.g., HOWES & RIDWOOD, 1888; ANDERSEN, 1978) believe that the first finger is quite simply the so-called prepollex. ANDERSEN presented myological evidence supporting this opinion. SHUBIN & ALBERCH (in press) suggest that the first finger may be represented by the prepollex or completely reduced.

RESULTS

The most plesiomorphic carpi have been observed in the Hyperoliinae (fig. 1a) but also in *Trichobatrachus* and *Cardioglossa* (fig. 1b). In this study, two members of the Astylosterninae (*Scotobleps gabomcus* (fig. 2a) and *Leptodactylodon ventrimarmoratus*) show the same configuration. But two other members of that primitive subfamily have a carpus composed of six bones similar to the plesiomorphic condition in Ranidae. Still, they both show traces of the ancestral configuration: *Astylosternus diadematus* (fig. 2b) has an indentation and *Nyctibates corrugatus* has a suture between the distal carpal 3 and the composite external distal carpal, so that the fusion is not complete yet. Unfortunately, we had only one specimen of each of these species.

In most of the ranids examined, the carpus has six elements, the distal carpal 3 being fused with the 4 and 5 (fig. 3a). This structure was described by HOWES & RIDWOOD (1888) for *Rana temporaria*, *R. arvalis*, *R. esculenta*, *R. alticola*, *Euphylyctis cyanophlyctus*, *Nannophrys ceylonensis* and *Platymanus vitianus*. It also occurs in many other ranids (*Conraua craspedes*, *Limnonyctes occipitalis*, *Phrynodon sandersoni*) and all species examined of the genus *Ptychadena* (*aequiplicata*, *christyi*, *chrysogaster*, *gubei*, *m. mascarensis*, *m. bibromi*, *perreti*, *porosissima* and *uzungwensis*). Interestingly, this primitive carpus also is present in the orophilius species of *Phrynobatrachus* (fig. 3c) such as *P. versicolor*, *P. krefftii* (LAURENT, 1941), as well as *P. petropedetoides*, *P. dendrobates*, and the giant species *P. acutirostris*, *P. sulfureogularis* and *P. asper*. South African *Phrynobatrachinae* (*Natalobatrachus bonebergi*, *Arthro-*

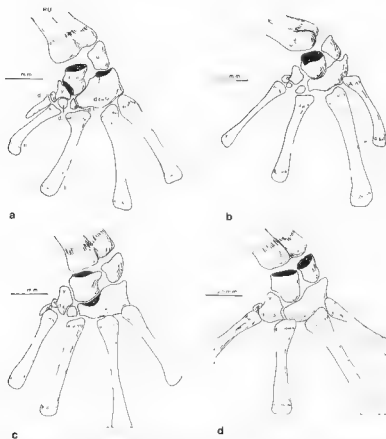


Fig. 1. — a: dorsal view of the carpus of *Hyperolius castaneus* (stage A); b: dorsal view of the carpus of *Cardioglossa cyaneospila* (stage A); c: dorsal view of the carpus of *Arthroleptus adolfriederici* (stage B); d: dorsal view of the carpus of *Schoutedenella pyrrosocelus* (stage C).

d2: distal carpal 2; d3: distal carpal 3; d4-5: external distal carpal 4 and 5 fused, believed by some authors to include a postaxial centrale; RU: radius and ulna; r: radial, u: ulnar; Y: Y element; II to V: metacarpals of fingers II, III, IV, and V.

leptella spp., *Cacosternum* spp., *Anhydrophryne rattrayi*) also have this carpal configuration. However, most *Phrynobatrachus* species have a highly derived carpus of only four elements (fig. 3d) in which the 2nd distal carpal and the Y element are fused with the external distal composite bone to form a single and large distal carpal. All lowland examined species of *Phrynobatrachus* are in this case as well as *Dimorphognathus africanus* from Cameroon.

Between the six-bone and the four-bone carpus, we of course can imagine an intermediate character state of five bones, in which only the 2nd distal carpal is incorporated into the external composite distal carpal, or else is fused with the Y element as in the arthroleptines. Such conditions might exist in some *Phrynobatrachus* species, but have not been observed so far. However, the arthroleptine configuration occurs in *Aubria subsigillata* (fig. 3b); moreover in a juvenile of this species, the cartilaginous carpus, the 3rd distal carpal is incompletely fused with the external composite bone.

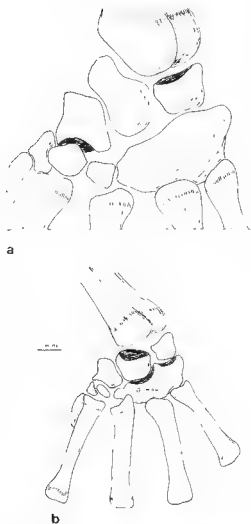


Fig. 2. - a: dorsal view of the carpus of *Scotobleps gabonicus*, without scale (stage A); b: dorsal view of the carpus of *Asylosternus diadematus* (stage D).

DISCUSSION

DREWES (1984) suggested that the primitive carpus of Hyperoliinae is actually a secondary condition owing to pedomorphosis, and therefore, a derived feature. His hypothesis

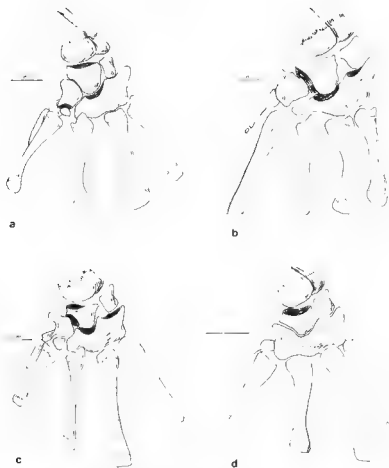


Fig 3. — a: dorsal view of the carpus of *Ptychadena chrysogaster* (stage D); b: dorsal view of the carpus of *Aubria subgillata* (stage E); c: dorsal view of the carpus of *Phrynobatrachus versicolor* (stage D); d: dorsal view of the carpus of *Phrynobatrachus natalensis* (stage F).

is made more plausible by his claim that no ranid possesses a free 3rd distal carpal; however, this claim is not true, because DREWES considered the Astylosterninae and Arthroleptinae to be ranids. There is, however, some merit in DREWES' idea, in the sense that the carpal elements in the Hyperoliinae are only superficially calcified. In a tadpole (stage 43 of GOSNER, 1960) of *Afraxalus osoroi*, calcification is absent, but the structure otherwise is the same as in the adult. Because this arrangement also occurs in *Scotobleps*, *Trichobatrachus* and *Lepidodactylodon*, no paedomorphic process is required to explain its occurrence in Hyperoliinae which supposedly derived from some Astylosterninae.

The apomorphic condition in the Astylosterninae subfamily is similar to the plesiomorphic configuration in ranids, in which the 3rd distal carpal is fused with the distal, external and composite carpal; however, the fusion is incomplete in *Astylosternus* and *Nycti-*

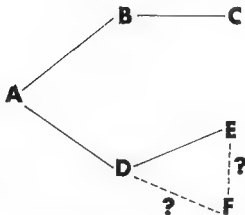


Fig. 4. — Evolution of the carpal stages in Ranoidea.

bates. This character state is widespread in anurans in general, e.g., Limnodynastinae, Bufonidae, Leptodactylidae, Hylidae (HOWES & RIDEWOOD, 1888; ANDERSEN, 1978). A five-bone carpus can be derived from a six-bone carpus by fusion of the 2nd distal carpal with the 3rd to 5th distal carpals, or with the Y element. The latter condition occurs in *Aubria* among ranids, as well as in the *Leptodactylus* species of the *cavicola* group and in the Dendrobatidae (HOWES & RIDEWOOD, 1888; ANDERSEN, 1978). The most apomorphic condition (4 bones) is characteristic of the lowland species of *Phrynobatrachus*, *Hemusus* (LAURENT, 1942) and some Microhylidae (HOWES & RIDEWOOD, 1888).

An altogether distinct evolutionary line is represented by the arthroleptines in which the most plesiomorphic state is found in *Cardioglossa*. The first derived step consists of fusion of the 2nd distal carpal with the Y element (e.g., *Arthroleptis*), and in the final stage, the 3rd distal carpal joins this *internal* and composite carpal (e.g., *Schoutedenella*).

CONCLUSIONS

Six carpal character states exist among ranoid frogs (fig. 4). State A is the most plesiomorphic (7 bones): radiale, ulnare, Y element, 1st, 2nd, 3rd distal carpals, fused 4th and 5th distal carpals (*Trichobatrachus*, *Scotobleps*, *Leptodactylodon*, *Cardioglossa*, and all Hyperoliinae).

In state B derived from A, the 2nd distal carpal merges with the Y element (*Arthroleptis*). In state C derived from B, the 3rd distal carpal also merges with the Y element (*Schoutedenella*). In state D, derived from A, the 3rd distal carpal merges with the fused 4th and 5th distal carpals (*Rana*, *Conraua*, *Euphlyctis*, *Limnonectes*, *Ptychadena*, primitive *Phrynobatrachus* species, *Phrynodon*, *Arthroleptella*, *Cacosternum*, *Anhydrophryne*).

In state E derived from D, the 2nd distal carpal merges with the Y element (*Aubria*). In state F derived from D or E, the Y element and all distal carpals merge to form a larger distal carpal (advanced, lowland *Phrynobatrachus* species, *Dimorphognathus*, *Hemusus*).

RÉSUMÉ

L'examen du carpe chez plusieurs espèces appartenant aux Astylosterninae, Hyperoliinae, Raninae et Phrynobatrachinae, confirme les hypothèses de LAURENT (1951). Le carpe le plus plésiomorphe qui ait été observé parmi les Ranoida est celui des Hyperoliinae, de quelques Astylosterninae et Arthroleptinae (*Cardioglossa*). A partir de cette structure, un premier clade se caractérise par la fusion du deuxième carpien distal avec l'élément Y pré-axial: ce sont les Arthroleptinae. Dans l'autre clade, le troisième carpien distal s'incorpore au carpien distal externe, déjà composite (4ème + 5ème carpiens). Ce sont les Ranidae, mais une transformation similaire s'est parallèlement réalisée chez *Astylosternus* et *Nyctobates*.

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APPENDIX

LIST OF SPECIMENS EXAMINED

Family ARTHROLEPTIDAE

Subfamily ASTYLOSTERNINAE

- Astylosternus diadematus*: FML 03215 (2 spécimens).
Leptodactylodon ventrimarmoratus: MHNG 1524/91 (1 spécimen), 1524/95 (1 spécimen).
Nyctobates corrugatus: MHNG 1525/26 (1 spécimen).
Scotobleps gabonicus: MHNG 1524/73 (1 spécimen), MHNG 1524/78 (1 spécimen)

Subfamily ARTHROLEPTINAE

- Arthroleptus adolfifrenedici*: RFL 90c (3 spécimens).
Arthroleptus variabilis: RFL 143 (1 spécimen).
Cardioglossa cyaneospila: RFL 66a (2 spécimens).
Cardioglossa leucomystax: RFL 170 (2 spécimens).
Schoutedenella pyrrhoscelis: RFL 121 (4 spécimens).
Schoutedenella sylvatica: RFL 169b (2 spécimens), RFL 43b (2 spécimens).

Subfamily HYPEROLIINAE

- Hyperolius castaneus*: RFL 54c (9 spécimens).
Hyperolius viridiflavus karissimbiensis: FML 3947 (2 spécimens).
Hyperolius marmoratus argenteiventris: RFL 101fg (2 spécimens).
Afraxalus laevis: RFL 16g (1 spécimen), RFL 92a (1 spécimen).
Afraxalus osorioi: RFL 4 (2 spécimens), RFL 74 (2 spécimens).
Afraxalus quadrivittatus: RFL 44b (2 spécimens).
Kassina senegalensis angehi: RFL 158g (1 spécimen).
Kassina senegalensis ruandae: RFL 273 (2 spécimens).
Phlyctimantis verrucosus: RFL 81b (3 spécimens), RFL 87 (3 spécimens).

- Leptopelis brevirostris*: MHNG 953/54 (1 spécimen), MHNG 548 (1 spécimen).
Leptopelis christyi: RFL 135 (4 spécimens), FML 3988 (1 spécimen), FML 3987 (1 spécimen).
Leptopelis kivuensis: FML 3989 (1 spécimen)

Family RANIDAE

Subfamily PHRYNOBATRACHINAE

- Dimorphognathus africanus*: MHNG 1031/43 (1 specimen), MHNG 1032/52 (1 spécimen).
Phrynobatrachus acutirostris: RFL C1 (2 spécimens).
Phrynobatrachus asper: RFL C18 (1 spécimen), RFL C5 (2 spécimens).
Phrynobatrachus dendrobates: RFL C10 (2 specimens).
Phrynobatrachus natalensis: RFL 438 (2 spécimens).
Phrynobatrachus petropedetoides: RFL C6 (2 specimens).
Phrynobatrachus sulfureogularis: RFL 346 (2 spécimens).
Phrynobatrachus versicolor: RFL 430 (2 spécimens).
Phrynodon sandersoni: MHNG 1560/40 (1 spécimen).

Subfamily RANINAE

- Aubna subsgillata*: RFL 209 (2 spécimen), RFL 212 (1 spécimen).
Conraua crassipes: RFL 246 (2 spécimens).
Lamnonectes occipitalis: RFL 348 (1 specimen).
Ptychadena aequiphacata: RFL 59 (1 spécimen).
Ptychadena christyi: RFL 76 (1 spécimen).
Ptychadena chrysogaster: RFL 141 (1 spécimen), RFL 143 (1 spécimen), FML 3947 (1 spécimen), FML 3949 (1 spécimen).
Ptychadena guibei: RFL 163 (1 spécimen), FML 3952 (1 spécimen), FML 3953 (1 spécimen).
Ptychadena mascareniensis bibroni: RFL C16 (2 spécimens).
Ptychadena mascareniensis mascareniensis: RFL 120 (2 spécimens), RFL 123 (1 spécimen), RFL 124 (1 spécimen), FML 3950 (2 spécimens).
Ptychadena perreti: RFL 72 (1 spécimen), RFL 99 (1 spécimen).
Ptychadena porosissima: RFL Cr1 (2 spécimens).
Ptychadena uzunguensis: RFL 157 (1 spécimen).
Rana albolabris: FML 3944 (5 spécimens).
Rana angolensis: FML 3992 (3 spécimens).